

OCTOCORAL RESEARCH— PAST, PRESENT AND FUTURE

BY

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When I was a small boy of five or so in New Jersey, my mother chanced upon the cocoon of a moth one autumn day and brought it home to keep it until it emerged, so I could see its miraculous transformation from an inert bundle of tawny silk threads to a gorgeous cecropia moth. I now think it was that event that sparked a lifelong interest in natural history. Later, growing up as I did in Florida, I was surrounded by all sorts of natural wonders and as a teenager I began collecting seashells, native orchids, and butterflies.

Before long I concentrated on shells because they were beautiful, many kinds were plentiful around southern Florida, and several well known conchologists lived in the area. Among them was Maxwell Smith, who had a large private collection and was author of several books on native and worldwide seashells for collectors. The famous malacologist, Henry A. Pilsbry of the Academy of Natural Sciences of Philadelphia, often visited Maxwell and his friends the McGinty brothers during his winter vacations. They were extremely helpful to me and several other budding conchologists including Gil Voss, whom I later came to know on a professional basis. With their help I became familiar with the common marine species, and I constantly barraged Harald Rehder, one of the curators at the Smithsonian Institution, with requests for identification of specimens that the local experts couldn't identify. The director of the Florida State Museum at the time, who was an avid shell collector and in need of cheap help cataloguing his specimens, even hired me during summer vacations to curate his collection at the museum in Gainesville.

While collecting seashells I became aware of the sea fans and sea plumes that dominate reefs in the Florida Keys. In the summer of 1941 I took a course in marine biology taught by F. G. Walton Smith at the University of Miami, which provided a more comprehensive view of marine life (Fig 1a), and in the fall I enrolled as a junior at the university. I had seen a little of the wide variety of gorgonians that abound on the reefs of Florida, but I was just a beginning student of marine biology at the university and they were the farthest things from my mind to consider for a research project or a thesis subject. At that stage in my education I easily could have been guided into entomology or tropical botany had my professors been sufficiently inspiring. But the only dynamic and enthusiastic teacher I had was Walton Smith, assistant professor of zoology and instructor in all aspects of marine biology, himself a student of the eminent English embryologist E. W. MacBride, so my interests began to focus on marine mollusks. I had learned the rudiments of invertebrate zoology in my first two years of college in Palm Beach, and during my junior year, 1941-42, Walton Smith opened up new vistas in marine zoology.



Figure 1. (a) Summer course in marine biology, University of Miami, July 1941 (photo by J.W. Mayer, University of Miami). Seated around table, clockwise from lower left: Bill Sutcliffe, May Smith, Christine Stenstrom, Helen Tierney, F.G. Walton Smith; standing l. to r., Herman Doochin, F.M. Bayer, Naomi Fork; (b) Drawing a Moorish Idol fish at Biak Island, April 13, 1945; (c) Elisabeth Deichmann at U.S. National Museum, 1954.

December 7 of that year changed many plans, mine included. I knew that military service inevitably would interrupt or terminate my college education. When the director of the Florida State Museum in Gainesville invited me to join the staff until I had to go into the military, I accepted my first full-time job. In less than a year I was drafted into the Army Air Corps and trained as a photographic technician, followed by an overseas assignment that took me to New Guinea, the Philippines and Okinawa. This provided an opportunity to collect mollusks and butterflies in the tropical Pacific. Personal acquaintance with exotic fauna and flora intensified my interest in natural history as a profession, although I really wasn't fully aware of it. My comrades-in-arms regarded me as something of a freak because I spent much of my free time on the reef collecting shells or in the nearby jungle catching butterflies. The only method of preservation that was practical under the circumstances was drying, so I made drawings of some of the items I couldn't preserve as dried specimens (Fig. 1b). The mollusks that I collected are now incorporated in the collections of the Department of Systematic Biology in the National Museum of Natural History.

Unlike many of my classmates I survived the war and was able to resume studies at the University of Miami. By then, Walton Smith had succeeded in establishing the Marine Laboratory of the University of Miami. When my interest in mollusks showed signs of persisting after the war, Walton advised me to look for a different subject to pursue. He had little time for shell collectors. In his opinion, shell collecting was for spinsters in the change of life and little old ladies in tennis shoes, not for the serious student of marine biology. About that time Walton was cultivating John Wentworth and his wife, a rich couple on Miami Beach who owned a powerful motor-yacht. They used it to dredge for shells and other marine creatures in the Straits of Florida and around the Bahama Islands. Among the specimens they collected were several resembling sea fans but quite unlike anything that grew on the reefs. Recognizing Walton's influence on my continuing education, I prudently decided to embark on an investigation of Alcyonaria. The only available comprehensive reference on the western Atlantic fauna was Deichmann's *Alcyonaria of the Western Part of the Atlantic Ocean* published in 1936 (Fig. 1c), which was based upon a huge unpublished monograph begun many years before by A. E. Verrill (Fig. 2a), the American pioneer in coral research. I quickly discovered that the Alcyonaria, now generally called Octocorallia because of the invariable octoradial symmetry of their polyps, are a taxonomic challenge even greater than the mollusks.

I didn't have time to get very far in my study of the gorgonians dredged up by the Wentworths, because I was invited by Waldo Schmitt, head curator of biology at the Smithsonian Institution, to apply for a position as assistant curator on the staff of the U.S. National Museum. As there were few candidates even moderately qualified so soon after the war, I was awarded the position. Dr. Schmitt, who was a specialist on Crustacea, had hoped to develop a new crustacean specialist for the zoological staff, but I persisted in working with alcyonarians. I imagine I was a major disappointment to him, although he never said so. As understanding and tolerant as he was, Dr. Schmitt did not pressure me to abandon my investigations on octocorals in favor of crustaceans. In my favor was the fact that the museum had a large collection of octocorals and other coelenterates but never had had a specialist to study them. Specimens always had been identified by collaborating specialists in other institutions, including A. E. Verrill, C. C. Nutting and Elisabeth Deichmann.



Figure 2. (a) Addison E. Verrill; (b) Elisabeth Deichmann and Frederick M. Bayer, Washington D.C., photo by L.B. Holthuis; (c) Kumao Kinoshita, Tokyo, about 1910; (d) Charles Cleveland Nutting, State University of Iowa.

Not long after I arrived at the U.S. National Museum in 1947, the Division of Marine Invertebrates was visited by Elisabeth Deichmann, curator of invertebrates at the Museum of Comparative Zoology of Harvard University, and the author of that vast monograph I had struggled with earlier in my efforts to identify gorgonians in Miami (Fig. 2b). Thus began a professional relationship and personal friendship that lasted the rest of Liska Deichmann's life. Eventually she became the external adviser and examiner of my doctoral dissertation, although officially Waldo Schmitt was my dissertation supervisor and advocate at my oral defense.

My first field assignment at the museum was to join an expedition to Bikini Atoll to survey the results of the atomic bomb tests that had taken place in 1946. My colleagues on the Scientific Resurvey of Bikini included Leonard Schultz, curator of fishes; J. P. E. Morrison, associate curator of mollusks; John Wells, professor of geology at Cornell University; and Harry Ladd and Joshua Tracey of the U. S. Geological Survey.

My immediate supervisor at the museum, Fenner Chace, was studying two genera of crabs that live in commensal association with stony corals, so I spent most of my time sloshing around on the reef flat with John Wells, collecting reef corals and documenting the crabs associated with them. It had been observed that the various species of crabs in the genus *Trapezia* differed in their color patterns. Having no camera but modest skills as a water-colorist, I took the opportunity to make sketches in life colors of the various color patterns of the specimens that I collected.

As I was not a skilled skin diver, I had no opportunity to collect alcyonarians other than a number of massive soft corals from the reef flat and back-reef trough. A Navy landing craft fitted for dredging, LCI 615, under the direction of R. Dana Russell, conducted several stations that obtained a number of interesting gorgonians. These formed the basis for my first published effort in the field of alcyonarian taxonomy.

Knowledge of the gorgonians of the Indo-west Pacific is scattered through the scientific reports of various expeditions beginning with the French Voyage of the *Astrolabe* 1826-29 under Dumont-Durville (Quoy & Gaimard 1833) and the *Vénus* 1836-39 under Dupetit-Thouars (Valenciennes 1846), which obtained only a few octocorals. The U.S. Exploring Expedition 1838-42 under Charles Wilkes obtained enough material for J. D. Dana (1846) to produce a comprehensive account of the Alcyonaria collected during the expedition along with species previously known. Dana reported the first specimen of precious coral, genus *Corallium*, collected in the Pacific, giving it the appropriate name *Corallium secundum*. Dana referred a problematic specimen to the fossil genus *Aulopora*, naming it *Aulopora tenuis* and classifying it in the family Tubiporidae because of its bright red skeleton.

Milne Edwards and Haime (1857) significantly advanced taxonomic knowledge of coelenterates in their *Histoire Naturelle des Coralliaires*, a comprehensive account of all anthozoans together with hydrocorals such as *Millepora* and *Stylaster*. This three-volume work, illustrated by an atlas of 31 plates, substantially extended Dana's treatment of zoophytes by including many species unknown to Dana as well as fossil species, which were not included in Dana's report for the U.S. Exploring Expedition. Volume 1 of this landmark work, devoted to the alcyonarians, antipatharians and zoantharians, incorporated for the first time Valenciennes' discovery of sclerites in the classification of alcyonarians. Volumes 2 and 3 were devoted to scleractinians and hydrocorals.

Several other authors reported on collections of more or less limited scope. Those geographically most pertinent to the Marshall Islands were by Kinoshita (Fig. 2c) (1907,

1908, 1909, 1910, 1913) on Japanese material, Nutting on Hawaiian and Japanese specimens (1908, 1912), and Versluys (1902, 1906, 1907) and Nutting (1910, 1911) (Fig. 2d) on the collections assembled by the Dutch *Siboga* Expedition in Indonesia. More cosmopolitan collections obtained during expeditions aboard H.M.S. *Challenger* (Wright & Studer 1889) and *Valdivia* (Kükenthal 1906, 1919; Kükenthal & Broch 1911) also could not be ignored in the context of that time.

With the help of this and other pertinent literature, I distinguished 12 species collected at Bikini, 4 of them new and one of them with a new “forma” (Bayer 1949). It was presumptuous for an inexperienced would-be taxonomist familiar only with gorgonians of the western Atlantic to describe and report on specimens from a vastly different faunal region. How many of the new species and new records reported in that paper will stand the test of time remains to be seen, but it now is clear that one of those new species probably is identical with a Japanese species described as new in 1906 by Versluys and again in 1908 by Kinoshita (Bayer 1982). The literature consulted in preparing this paper clearly demonstrated the superficiality and inadequacy of illustrations of taxonomic characters, and I resolved not to perpetuate that mistake. The only advance in octocoral taxonomy to which I can lay legitimate claim is the quality of illustrations that accompany descriptions of species even if not established as new.

About that time, Ray Moore of the University of Kansas invited me to contribute a chapter for Part F of the newly established series *Treatise on Invertebrate Paleontology*. For that volume Ray Moore retained the name “Coelenterata” for the phylum, contrary to Libbie Hyman’s preference for “Cnidaria.” In it I defined and illustrated all the genera recognized at the time and replaced Dana’s name “Alcyonaria” with Haeckel’s term “Octocorallia” (Bayer 1956).

Beginning in 1950, the Office of Naval Research sponsored a program of Scientific Investigations of Micronesia (SIM) administered through the Pacific Science Board of The National Academy of Sciences. SIM conducted a series of expeditions to Pacific atolls, including Arno in the Marshall Islands, Onotoa in the Gilbert and Ellice Islands, Raroia in the Tuamotus, Ifaluk in the Caroline Islands, and Kapingamarangi, one of the southernmost Carolines. The Pacific Science Board established the Atoll Research Bulletin as a vehicle to publish the results of these expeditions and information about atolls and coral reefs in general. Beginning in 1950 under the editorship of F. R. Fosberg, the Bulletin has now reached its golden anniversary under the editorship of Ian G. Macintyre.

Relatively few octocorals were collected during the SIM expeditions, but as a member of the team that surveyed Ifaluk in 1953 (Fig. 3a) I obtained several specimens of a very unusual gorgonian that I later described as a new species, genus, and family of Holaxonia (now placed in Calcaxonia) called *Ifalukella yanii*, family Ifalukellidae. As I was already halfway around the world, I returned to Washington via Japan, where I hoped to find the type specimens described by Kinoshita. A young Japanese foreign service officer who had translated some of Kinoshita’s papers in Japanese while a student at Georgetown University, now back in Tokyo, was of immeasurable assistance in my search. I was partly successful in that goal but, more important, two of my Japanese colleagues, Dr. Itiro Tomiyama and Dr. Tokiharu Abe, who were official research collaborators for Emperor Showa, arranged for us to visit the Emperor’s biological laboratory, which contained a great many specimens for the most part personally collected. Although interested in biology in general, the Emperor’s serious research



Figure 3. (a) SIM Expedition to Ifaluk Atoll, Caroline Islands, 1953. Standing (l. to r.) Ted Arnow, U.S. Geological Survey; Donald P. Abbott, Stanford University; Joshua I. Tracey, U.S. Geological Survey; seated (l. to r.) Robert R. Harry (now Rofen), Stanford University; Frederick M. Bayer, Smithsonian Institution; (b) Octocoral (*Sarcophyton*) photographed underwater at Palau, 1955; (c) Photographing reef fauna underwater at Palau Islands, 1955.

interest was on hydroids. After touring the laboratory we were invited to a private audience with the Emperor. He was aware of the large collection of corals in the Smithsonian and wished to know more about it. It was an extraordinary and unforgettable meeting for an obscure American biologist and a young Japanese foreign service officer. However, in Washington after the fact it was considered a breach of diplomatic protocol: it was not proper for an employee of the U.S. Government to meet a foreign head of state without first notifying the State Department. An unexpected result of that event was several subsequent meetings with the Emperor during later visits to Japan (also without prior approval of the State Department), and he visited my department and my lab during his official state visit in 1975 (Fig. 4).



Figure 4. Emperor Showa examining specimens in Department of Invertebrate Zoology, Smithsonian Institution, October 2, 1975. With F.M. Bayer, Joseph Rosewater, and Prof. H. Sato, interpreter.

Also with support from the Office of Naval Research, the George Vanderbilt Foundation at Stanford University sent an expedition to the Palau Islands in 1955 to collect and study the marine fauna (Fig. 3b,c) (Bayer & Harry-Rofen 1957). I was able to obtain a substantial collection of octocorals, including three specimens of Dana's *Aulopora tenuis* (now *Cyathopodium tenue*), an inconspicuous but highly interesting species that had not been collected since Dana described it in 1846 (Bayer 1981).

P. Wagenaar Hummelinck, a Dutch zoologist who collected extensively in the Caribbean islands, sent me his large collection of gorgonians from the Netherlands Antilles for identification. To determine the species in the Hummelinck collection it was essential to resolve the many taxonomic problems in the existing literature on that fauna.

Because travel to foreign museums to examine type specimens was not feasible in those days, it was necessary to evaluate the numerous species from their cursory and often unillustrated descriptions. Verrill had obtained slide preparations of a few type specimens in European museums, and Liska Deichmann herself had seen and made notes on other specimens during visits to Europe. Working with this shaky foundation, often in consultation with Liska during her many visits to Washington, I produced a report on the Hummelinck collection supplemented by previous and new collections of the U.S. National Museum and Museum of Comparative Zoology that satisfied both Dr. Hummelinck and my dissertation committee at The George Washington University. After three years in press, it was published (Bayer 1961/62) both as a trade book by Martinus Nijhoff in The Hague, and as volume 12 in the series *Studies on the Fauna of Curaçao and Other Caribbean Islands*, identical except for the preliminary leaves and page 1. In the interests of bibliographic and nomenclatural accuracy, I should point out that the official copyright date of the trade book is 1961. Because the journal version published by Natuurwetenschappelijke Studiekring voor Suriname en de Nederlandse Antillen was not distributed until January 1962, new taxa and nomenclatural acts date from the trade book issued in 1961.

That work covers the shallow-water fauna of the same geographical area considered in Deichmann's report on the deep-water fauna. Although subsequent collections have revealed all too clearly its inadequacies, it has remained for four decades the only taxonomic work on octocorals of warm western Atlantic waters. Many specimens later obtained by scuba diving on deep reef slopes, as well as collections from previously unsampled localities, are difficult to identify with any certainty and suggest a degree of individual, ecological, bathymetric and geographic variation that I could not take into account.

Although I divided the huge number of specimens examined during preparation of my paper ("monograph" is too pretentious) into 101 species, they now clearly reveal that not all specimens of any given species are exactly alike. Too many are "just a little different" from the diagnoses of the species; they don't fit neatly into the preconceived notion of the species. This suggests that morphological variation might be induced by environmental factors. An opportunity arose to join the faculty of my old alma mater and I thought it would provide opportunities to study living populations of gorgonians in different habitats to determine how species vary. Early in 1962 I left my position at the museum to become a professor of marine science at the University of Miami with plans to tackle the problem of ecological variation through experimentation in the field. I embarked upon an ambitious and, as it turned out, unrealistic program of transplanting parts of colonies from one habitat to another. This involved cementing them on concrete tiles and installing them in areas of the reef where water currents differed from those of the reef where the colonies grew originally. I had not reckoned with the inquisitive nature of skin divers, and as rapidly as I established a series of tiles for transplant experiments they were disturbed or removed by persons unknown.

Under the direction of Gilbert Voss, the University of Miami began a research project in deep-sea biology involving a program of trawling in the Straits of Florida and Caribbean Sea using a North Sea-type fishing trawler, *Gerda*, outfitted for scientific dredging and trawling. This program expanded substantially with the acquisition of oceangoing research vessels, first the *John Elliott Pillsbury* (Fig. 5), later the *James M. Gilliss* and then the *Columbus Iselin*. Operations from these vessels obtained vast



Figure 5. R/V *John Elliott Pillsbury* about 1965.

numbers of marine animals from the tropical western Atlantic, the Bay of Panama, and the coast of West Africa, including a rich collection of octocorals as well as other invertebrates and fishes. Operations aboard R/V *Gerda* in 1963 obtained the first records of the precious coral genus *Corallium* in the tropical western Atlantic, as the new species *Corallium vanderbilti* reported by Boone (1933) was based upon a specimen of *Dodogorgia nodulifera* (Hargitt), a species with gross aspect deceptively similar to *Corallium* but lacking the stony axis characteristic of that genus (Bayer 1964).

The variety of gorgonians and other octocorals we collected in the western Atlantic was far greater than Deichmann had included in her monograph. With new collections arriving after every cruise it was impossible to keep up with new discoveries, so I confined my taxonomic work on octocorals to investigation of material from Antarctic waters obtained by naval operations in the 1960s and transmitted by overseeing agencies including Stanford University and the Smithsonian Oceanographic Sorting Center.

I had not bargained for the amount of time required to meet teaching commitments in an academic environment, and to apply for grants from funding agencies to support research. Neither was I prepared for the complications involved in doing taxonomic research away from comparative collections. Over a period of more than 10 years I was able to publish only two short papers on gorgonians, an unacceptable level of productivity. Knowing that taxonomic work depends upon comprehensive research collections not present in Miami, I had maintained an association with the museum through an appointment as Smithsonian research associate. During 1971 and 1972 I took

a year's leave of absence from the University to occupy a visiting curatorship at the Smithsonian Institution that allowed me to make some inroads on western Atlantic octocorals from the Miami collections as well as some Antarctic material, and to lay the groundwork for a permanent return to the Smithsonian. In 1975 I rejoined the museum staff in a temporary curatorship later made permanent by the museum director at the time, Porter Kier, himself an accomplished taxonomist who worked on living and fossil echinoderms.

The discovery of biologically important compounds in octocorals, such as the prostaglandins reported by chemists at the University of Oklahoma (Weinheimer & Spraggins 1969), intensified biochemical investigation of these widespread marine animals and dramatically increased the demand for identification of species under study. This increased demand has far outstripped the capacity of the few active taxonomists to carry the load. In 1950, the *Zoological Record* reported 7 taxonomic papers by 3 authors, none dealing with biochemistry. In 1970 the *Zoological Record* reported 6 papers by 6 authors or author-teams on the biochemistry of octocorals, but only 7 taxonomic papers by 5 authors. In the twelve-month period spanning 1997-98, 30 authors and author-teams published 45 papers on biochemistry; but only 10 authors published 11 taxonomic papers during the same period.

In 1980 I was awarded a Senior Queen's Fellowship to Australia, where I was a guest at the Roche Research Institute of Marine Pharmacology at Dee Why, near Sydney. The Roche Research Institute was interested in the identification of octocorals for possible exploitation of their bioactive compounds. While at Roche, Phil Alderslade and I studied hundreds of specimens of gorgonians of the families Melithaeidae and Paramuriceidae, both major components of the octocoral fauna of the Great Barrier Reef. Six genera of Melithaeidae and about 22 of Paramuriceidae are accepted as valid, most with numerous nominal species common around Australia. Although we found groups of "species" roughly equivalent to the known genera in both families, it was virtually impossible to detect significant morphological discontinuities for separating genera, and the traditional characters used in the delimitation of species seemed to merge imperceptibly. We concluded that specimens in those two families formed what amounted to morphological continua without tangible discontinuities that could be used to delimit "species" consistently. Neither geographic nor bathymetric data for the specimens yielded information that would help in recognizing species. Some specimens corresponded nicely with species described in the literature, but in most cases they intergraded with adjacent species to such an extent that it was impossible to draw a definite line of demarcation.

An important outcome of my stay at Roche was the decision to hold an international workshop on Octocorallia in 1981 at the Australian Institute of Marine Science at Townsville (Bayer 1982). One tangible result of that workshop, attended by Jaap Verseveldt (The Netherlands), Manfred Grasshoff (Germany), Steven Weinberg (The Netherlands), Philip N. Alderslade and John Coll (Australia), Katherine M. Muzik (USA and Japan), Shohei Shirai (Japan) and others (Fig. 6), was the first draft of a trilingual glossary of anatomical terms used in the description of octocorals, which eventually was published in the Netherlands (Bayer, Grasshoff & Verseveldt, eds. 1983).

Recognizing the need for increased expertise in identifying octocorals, UNESCO sponsored the First Octocoral Research Workshop and Advanced Training Course at Phuket, Thailand, November 30 to December 13, 1987. Under the guidance of Philip



Figure 6. International Workshop on Octocorallia, September 1981, Australian Institute of Marine Science, Townsville, Queensland. Standing, l. to r., M. Mahendran (Sri Lanka), Stephane LaBarre (Australia), P.N. Alderslade (Australia), Manfred Grasshoff (Germany), Shohei Shirai (Japan). Seated, l. to r.: J. Verseveldt (The Netherlands), Katherine Muzik (U.S.A and Japan), F.M. Bayer (U.S.A.), Zena Dinesen (Australia), Steven Weinberg (The Netherlands).

Alderslade, Y. Benayahu, and Katherine Muzik, participants from Indonesia, Malaysia, Papua New Guinea, the Philippines, Sri Lanka and Thailand learned methods of collecting, preserving, and curating octocorals, as well as the basic techniques of taxonomic identification. One of the conclusions of that workshop was the often-repeated observation that Southeast Asia, like the rest of the world, is lacking in trained personnel and basic research in the field of octocoral taxonomy.

In the absence of a comprehensive monograph of the world octocoral fauna, biochemists and taxonomists in many parts of the world continue to experience great difficulty in determining species of octocorals. The number of species recorded in the literature is too great to be confirmed, defined and illustrated in a comprehensive, reliable treatment consistent with modern taxonomic procedures.

The first monograph of worldwide “zoophytes,” the category that included octocorals, was published more than two centuries ago by Peter Simon Pallas (1766), who reported a total of 31 species of octocorals along with the sponges, hydroids, stony corals, actinians, bryozoans, and “ambiguous genera” that included parasitic worms, *Volvox*, and coralline algae. Lamarck (1816) increased the number to 124 species, and a treatise by Lamouroux (1816), confined to the “polypiers coralligènes flexibles,” included 163 nominal species of octocorals.

In a work on the corals of the Red Sea, Ehrenberg (1834) proposed a dual classification distributing the zoophytes between two orders, Zoocorallia for soft-bodied or unattached forms divided into three Tribes, and Phytocorallia for attached forms

divided into seven Tribes. In this ingenious but unnatural system, octocorals were split between Zoocorallia (the Pennatulacea and Alcyonacea) and Phytocorallia (all of the Gorgonacea, with *Heliopora* grouped with *Millepora*).

The most significant advance in octocoral classification was made by Valenciennes (1855) in the abstract of a larger, more detailed monograph that never was published. Although John Ellis (1755) published the first--and remarkably accurate--drawings of the "Figures of hollow Crosses" in the cortex of the scleraxonian *Corallium rubrum* (Fig. 7), Valenciennes was the first to observe that these calcareous structures, which he called "sclerites," in the soft tissue of various gorgonians differed in shape from species to species. He established several genera of octocorals on the basis of such differences, many of which are still recognized today.

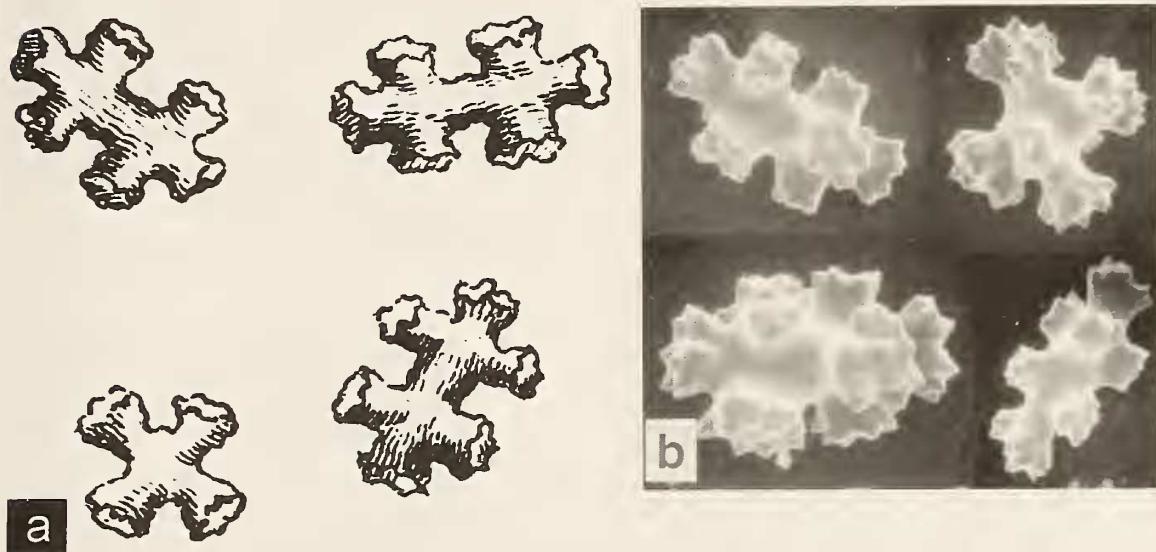


Figure 7. (a) Sclerites of *Corallium rubrum* as drawn by John Ellis, 1755; (b) same as photographed under scanning electron microscope at Smithsonian Institution, 1994.

Although Milne Edwards and Haime (1857) incorporated Valenciennes' observations on sclerites in their classification of octocorals in which they recognized 197 species based for the first time upon objective criteria and beginning the "modern" era of octocoral taxonomy, it remained for Kölliker (1865) to publish illustrations of many of the kinds of sclerites described by Valenciennes. Since that time, sclerites have become a principal character for the description, identification and classification of octocorals.

Recognition of sclerites as an important feature for defining and identifying octocorals by no means minimized the need for accurate depiction of colonial form. Today we can look back with admiration at illustrations of octocoral colonies produced by naturalists before the taxonomic value of sclerites was discovered. The magnificent encyclopedia of "Pflanzenthier" (Esper 1788-1830), containing hundreds of hand-colored engravings, illustrated for the first time colonies of many key species of gorgonians. The exquisite engravings of the few gorgonians collected by the French vessel *Vénus* (Valenciennes 1846) are meticulously accurate and are unequaled even by present standards.

By the end of the nineteenth century the number of octocorals had become so unmanageable that monographs on a worldwide scale were impractical. Major contributions to knowledge of octocorals were contained in the reports of major scientific expeditions such as that of H.M.S. *Challenger* (Wright & Studer 1889), R.I.M.S. *Investigator* (Thomson & Henderson 1906; Thomson & Simpson 1909), the Dutch research ship *Siboga* (Versluys 1902, 1906, 1907; Nutting 1910, 1911; Stiasny 1935, 1937) (Fig. 8a), and several smaller expeditions in various parts of the world.

Recognizing a need for an overall revision of the octocorals known so far, Kükenthal began a series “Versuch einer Revision der Alcyonaceen” (1902, 1903, 1905, 1907), which he never completed, although he published a number of shorter papers giving his ideas of the “System und Stammesgeschichte” of individual families, and a new classification of octocorals (1921). Nine years later, Hickson (1930) published his own classification of the Alcyonaria.

Kükenthal (1906, 1919), together with a few of his students and his Norwegian colleague Hjalmar Broch (Kükenthal & Broch 1911), published a comprehensive account of the octocorals collected by the steamer *Valdivia* during the German Deep-sea Expedition 1898-99. His summaries of the known genera and species of Pennatulacea (Kükenthal 1915) and Gorgonacea (Kükenthal 1924) are the nearest things to monographs of major octocoral taxa available today. Kükenthal recognized a world total of 141 certain and 134 doubtful species of Pennatulacea, and 805 certain and 255 doubtful species of Gorgonacea. A substantial number of species have been described in subsequent years, but 1,500 species would be a conservative total for those two orders of Octocorallia. Assuming a similar number of species for the soft corals and stoloniferans, which have not been summarized as Kükenthal did for the gorgonians and sea-pens, the number of valid species of octocorals could reasonably be estimated at about 3,000.

Regional monographs have been published recently for some geographical areas for which collections are reasonably complete (New Caledonia: Grasshoff 1999; Red Sea: Grasshoff 2000; Mediterranean: Carpine & Grasshoff 1975, and Weinberg 1976, 1977, 1978; eastern Atlantic: Grasshoff 1992). However, such regional works have an inherent limitation that can be underestimated if they are used to identify specimens from other geographical regions. Years ago, one novice complained to me that Deichmann’s monograph of western Atlantic Alcyonaria resulted in incorrect identifications of specimens from the Pacific coast of the Americas.

Current literature is adequate for the reliable identification of most octocoral species of shallow and moderate depths in the Mediterranean and eastern Atlantic, but specimens from deep water still may be difficult to determine. To a lesser extent the same is true of the western Atlantic, although the only account of the shallow-water fauna is seriously out of date. Octocorals of the eastern Pacific, the Indo-west Pacific, and Southern Ocean present a greater problem. The only comprehensive treatment of the shallow-water octocorals of the Pacific coast of the Americas is in serious need of revision (Verrill 1868-69), and the deep-water fauna has been investigated only along the coast of California and that in a very superficial and inadequate way (Nutting 1909). Shallow-water species from this entire region can be identified, but with doubtful accuracy, while deep-water specimens remain problematic.

Octocorals are poorly represented in the shallow waters of the Hawaiian Islands, and the deep-water species have been reported incompletely (Nutting 1908; Bayer 1952, 1956). Some species of this fauna can be identified with reasonable reliability, but others



Figure 8. (a) Gustav Stiasny at Rijksmuseum van Natuurlijke Historie, Leiden; (b) Jakob ("Jaap") Verseveldt at Zwolle, The Netherlands, 1984; (c) Philip Alderslade at Townsville, Australia, 1981; (d) Manfred Grasshoff at Townsville, Australia, 1981.

are inadequately known.

The vast expanse of the western Pacific is a veritable *terra incognita* of octocorals except for the principal soft coral genera that have been revised by Verseveldt (1980, 1982, 1983, 1988) (Fig. 8b) and the gorgonacean family Isididae (Alderslade 1998) (Fig. 8c). Otherwise, isolated specimens can be identified only by reference to widely scattered reports that leave many questions unanswered. Much Japanese material now can be identified with some degree of certainty, as the octocoral fauna has been investigated by several authors (Kükenthal 1908, 1909, 1910), Kinoshita 1908, 1909, 1910, 1913; Nutting 1912; Balss 1910; Aurivillius 1931; Utinomi 1952, 1954, 1957, 1960, 1961, 1966, 1976, 1977, 1979). Information on the octocorals of the Philippines, the islands of the tropical North and South Pacific, and most of the Indian Ocean and Red Sea is scattered among expedition reports, independent papers in scientific journals, and monographs of families or genera.

The octocoral fauna around the continental landmass of Africa that extends toward the Southern Ocean was studied by Hickson (1900, 1904), J. Stuart Thomson (1910, 1911, 1915, 1917, 1923) and, most recently, by Williams (1989, 1992a, 1992b, 1993). Little is known about the octocorals of the southern tip of South America. Studer (1879) reported on a few species of octocorals obtained in the vicinity of the Straits of Magellan by a German expedition aboard S.M.S. *Gazelle*, and specimens collected by H.M.S. *Challenger* at a number of stations in the area were described by Wright & Studer (1889), but the octocoral fauna as a whole is inadequately known.

Octocorals of the Southern Ocean have been described in numerous independent papers covering a few species or limited taxonomic groups, as well as in reports of Antarctic expeditions (e.g., Gray 1872: *Erebus and Terror*; Hickson 1907: National Antarctic Expedition; Kükenthal 1912: Deutsche Südpolar Expedition; Thomson & Rennet 1931: Australasian Antarctic Expedition), but so far no attempt has been made to revise and monograph the entire fauna with detailed synonymies that correlate information scattered through an extensive literature.

In retrospect, I can now look back on the 100 or more papers I have published on the octocoral fauna worldwide and ask: "What did I really accomplish toward alleviating the deficiencies of taxonomic information?" I am compelled to answer: "Not much." My article on Octocorallia in *The Treatise on Invertebrate Paleontology*, the handbook of shallow-water octocorals of the West Indian region (1961/62), and the key to genera of Octocorals excluding the Pennatulacea (1981) may have clarified some problematic aspects of octocoral taxonomy, but for the most part I have only added bricks to a structure that has yet to be designed and built. About all I can say with any satisfaction is that I have set new standards for illustrating taxonomic descriptions that should make them much more accurate, and identifications much more reliable in the future. The development of scanning electron microscopy and its adaptation to research on octocoral taxonomy would have resulted in new standards in any case, but I believe that I was the first author to publish a description of a new species illustrated with scanning electron micrographs (Bayer 1973). Since that time, most authors have followed suit. Until the year 2000, it was accepted that the mineral of all gorgonians having mineralized axes was calcium carbonate, either calcite or aragonite, depending upon suborder or family, and in some families the supporting axes were described as "purely horny." Through a very rewarding collaboration with geologist Ian Macintyre, some peculiar structures found in the organic axis of several genera in the family Gorgoniidae were found to be neither

calcite nor aragonite, but carbonate hydroxylapatite (Macintyre et al. 2000). Further study revealed that the mineral of all genera and species of the family Gorgoniidae having mineralized axes was carbonate hydroxylapatite (Bayer and Macintyre 2001), a unique taxonomic characteristic.

New techniques of molecular analysis are opening up exciting possibilities for arriving at solutions to the problem of fitting evolving concepts of species and genera that vary with geographical and ecological conditions over great distances into a taxonomic framework based upon the idea of morphologically distinct taxa. Although a completely revised monograph of the western Atlantic fauna still does not exist, comprehensive collections of both shallow-water and deep-water specimens are more than adequate for such a monograph are now on hand. Collections also are now available to support a thorough description of the deep-water fauna of the Pacific coast of the Americas and a review of the shallow-water Panamic fauna. Similarly, enough material exists in several museums around the world to attempt a complete analysis and revision of the octocoral fauna of the Southern Ocean. Although I did produce a few papers that clarified the status of a few Antarctic forms (Bayer 1990, 1996a, 1998), others merely added to the taxonomic overburden and remain to be incorporated in an overall synthesis (Bayer 1950, 1980, 1988, 1993a,b, 1996b, 1998; Bayer & Stefani 1987).

From a purely practical standpoint, one of the most pressing needs today is for a comprehensive study to discriminate species and determine such points where lines can be drawn to discriminate genera, families and, where necessary, suborders and orders. Grasshoff's (Fig. 8d) exemplary work on the shallow-water fauna of New Caledonia, the Red Sea, and the eastern Atlantic are fundamental building blocks in this direction. The literature is now so large and type material scattered among so many collections worldwide that a monograph of world Octocorallia is still an impossible dream. Smaller regional revisions, with their inherent inconsistencies and disagreements, may be the most that can be achieved for the time being.

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